

## A Guide to the Identification of the Harvestmen (Arachnida: Opiliones) of Maryland

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**Abstract** - A taxonomic key, diagnoses, and geographic distributions are provided for the 24 species of harvestmen that are known from or are likely to occur in Maryland. Twenty species are documented, with records of *Caddo agilis*, *Phalangium opilio*, *Odiellus pictus*, *Leiobunum flavum*, and *Vonones sayi* published for the first time. Four additional species—*Acropsopilio boopis*, *Crosbycus dasyncnemus*, *Leiobunum cretatum*, and *Sabacon cavicolens*—are expected to occur in Maryland but have yet to be recorded. Due to misidentifications or other taxonomic issues, 2 species (*Hadrobunus grandis* and *Leiobunum crassipalpe*) have been reported erroneously from the state and another (*L. speciosum*) may be a color variant of a widespread species, *L. vittatum*. Additional species may yet emerge, primarily through new systematic analyses or unanticipated range extensions of known taxa. The key uses many new characteristics, including those that substantially improve the identification of females. Information on the collection, preservation, rearing, dissection, and identification of harvestmen is summarized.

### Introduction

Members of the arachnid order Opiliones, or harvestmen, are among the most visible terrestrial arthropods, but even most arachnologists cannot reliably assign a species name to a specimen. Like many other invertebrates, the ecological significance of harvestmen is largely unknown, and remarkably little research has been devoted to understanding their biology, including their taxonomy (Pinto-da-Rocha et al. 2007). The most recent taxonomic catalogs to encompass the harvestmen of the United States (Cokendolpher and Lee 1993, Kury 2003), taken together, record 16 species from Maryland, including some that clearly do not occur in the state or are otherwise problematic. The present work documents 20 species, with 5 published here for the first time, and anticipates the presence of 4 additional species based on their occurrence in surrounding states. Future work will likely alter the taxonomic composition of Maryland's harvestman fauna even further. Recent phylogenetic work (Hedin et al. 2012) indicates that the names *Leiobunum*, the most diverse genus in the state, and *Nelima* will eventually apply only to certain European species, with most North American harvestmen requiring new generic names. The species currently recognized as *Leiobunum formosum* auct. will be transferred to *Hadrobunus* for similar reasons (Burns et al. 2012). Taxonomic revisions of the widespread and morphologically variable species *Leiobunum calcar* (Wood), *L. politum* (Wood), and *L. vittatum* (Say) may result in 2 or more species

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added to the state list. Finally, it is possible, though less likely, that increased sampling in the under-studied Delmarva Peninsula and mountainous western counties will reveal additional species through unanticipated range extensions. Aside from phylogenetic analyses or taxonomic revisions, caves are the most likely source for new, undescribed species (e.g., Shear 2010).

## Summary of Methods for the Study of Harvestmen

### Collection and preservation

Harvestmen can be found in most terrestrial habitats in Maryland, with the greatest diversity occurring in and at the edges of mesic forests. Adults of the familiar daddy-longlegs type (mostly *Leiobunum*) can be found resting or moving about on herbaceous vegetation, shrubs, tree trunks, leaf litter, etc. from May to December, with the greatest species diversity occurring in mid-summer. A canvas sweep net can be useful in collecting harvestmen, both by standard sweeping or, given their penchant to escape by falling, by placing the net below a specimen and invoking an escape reaction. With practice, one can become proficient in capturing specimens from vegetation with fingers. The goal is to grab the body and/or the bases of several legs. Although most long-legged harvestmen can detach their legs, the animal needs to exert leverage across the trochanter-femur joint and this cannot be accomplished with all legs unsupported. There are relatively few exclusively nocturnal species (e.g., *Hadrobunus maculosus* (Wood) [Fig. 36]), but these can often be found during the day under fallen bark, loose stones, etc. Still, night collecting may reveal a somewhat different harvestman fauna. Pitfalls can be effective in obtaining large numbers of specimens, but the catch will be heavily biased toward a few ground-dwelling forms, and experience has shown that climbing species may be missed entirely (e.g., Draney and Shultz 2016).

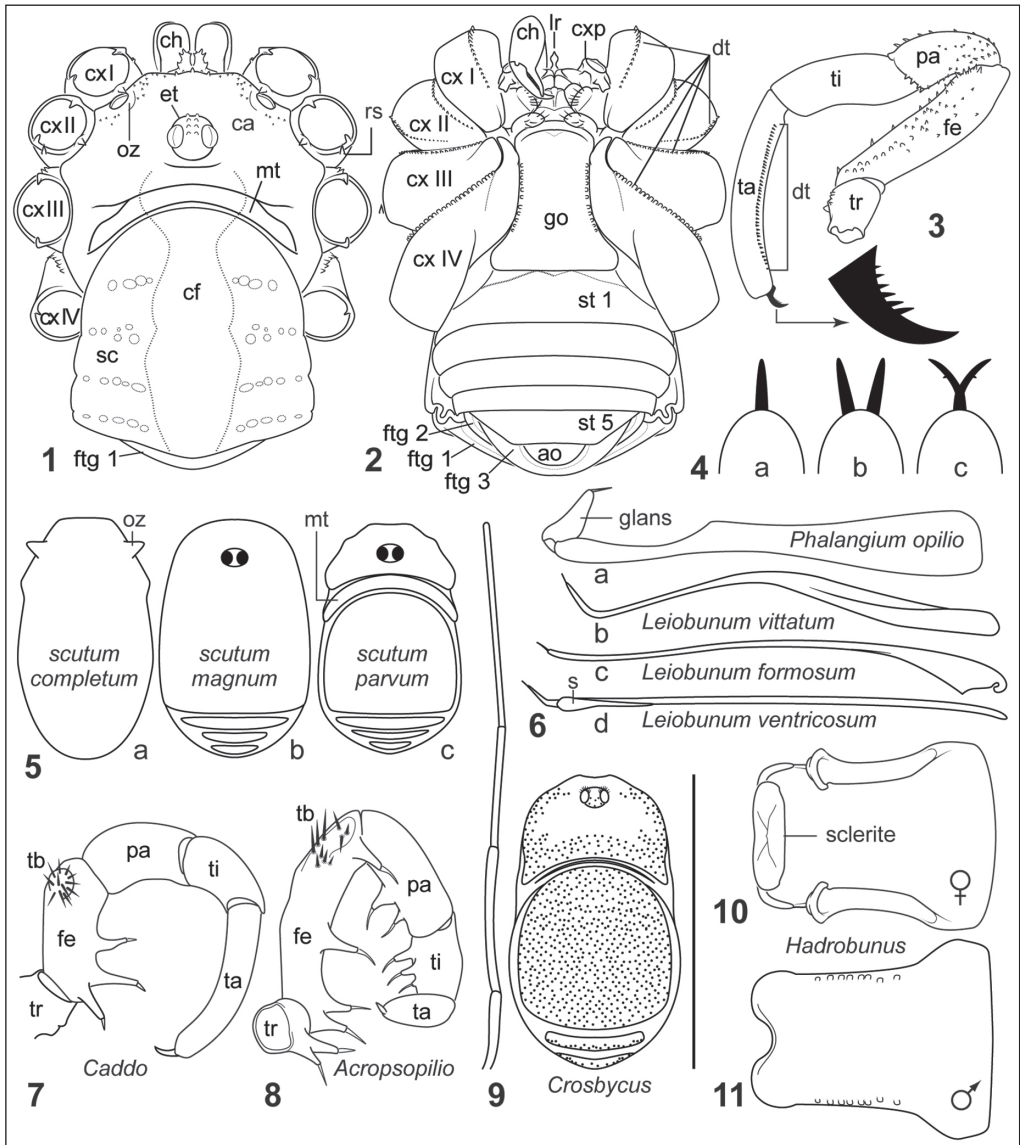
There is a small, understudied fauna of litter-dwelling forms in Maryland that includes most of the species still expected, but not yet known, in the state—*Acropso-pilio boopis* (Crosby) (Fig. 32), *Crosbycus dasyncnemus* (Crosby) (Fig. 9), *Sabacon cavicolens* (Packard) (Fig. 34)—and poorly represented higher taxa, including the cyphophthalmid *Siro exilis* Hoffman (Figs. 28, 29) and the travuniid *Erebomaster acanthinus* (Crosby and Bishop) (Fig. 31). These species are best found by turning objects on the ground, sifting litter, or through Berlese or pitfall sampling.

Preservation in vials containing 70–75% ethanol with a drop of glycerin is standard, although 50% isopropanol can also be used. Higher concentrations of alcohol result in greater dehydration and stiffening of tissues, which greatly increases the likelihood of damage through handling, especially the loss of legs.

### Rearing

No lab cultures of native harvestmen appear to exist, although several workers have had success with the non-native *Phalangium opilio* L. (Figs. 37, 38) (Klee and Butcher 1968). However, rearing individuals from any free-living stage to adulthood is relatively simple, at least for species of *Leiobunum*. A size-appropriate enclosure should be well ventilated to minimize mold-inducing humidity, but water should be

readily available; a water-filled vial resting on its side and stoppered with a wick of moist cotton works well. Dried food intended for predatory fish, hermit crabs, or frogs are good sources of nutrition but may have to be pulverized to an appropriate size for tiny instars. Food can be provided ad libitum but must be kept dry and removed at the first sign of mold; likewise, the cotton of the water vial should be replaced if it gets moldy. It is imperative that all immature stages be provided with a surface on which to molt; ecdysis cannot be completed successfully on the smooth floor or walls of a plastic or glass container. A piece of fabric or screen mounted as a vertical surface is sufficient. Most *Leiobunum* species can tolerate multiple individuals in the same enclosure as long as they are not in constant contact. The space available in a terrarium



Figures 1–11. [Caption on following page.]

can be enhanced by wadding nylon screen to increase the surface area available for climbing and perching. Soil or moist *Sphagnum* can be provided for oviposition.

### Dissection of genitalia

Characters associated with genitalia and other sexually dimorphic features tend to be the most useful in identifying species. In freshly dead specimens, the genital operculum can be opened readily and the penis can be withdrawn carefully using forceps. However, this approach can cause significant damage once tissues have stiffened due to preservation in alcohol. Instead, a scalpel or hypodermic needle can be used to cut the cuticle between the lateral margin of the genital operculum and medial margin of coxa IV (see Fig. 2). The operculum can then be opened like a trapdoor with a posterior hinge or the operculum can be removed by continuing to cut along the posterior hinge (e.g., Fig. 23), which, in most cases, will expose the distal end of the penis in males or the sternum and anterior inner lip of the operculum in females. If the penis can still not be extracted by a weak tug with forceps, one can make a longitudinal slice through the abdominal sternites to extract the penis and associated sclerites and muscles. The practice of squeezing the abdomen of living specimens to evert the penis prior to preservation (Weed 1887) results in significant damage and distortion of key parts and is discouraged.

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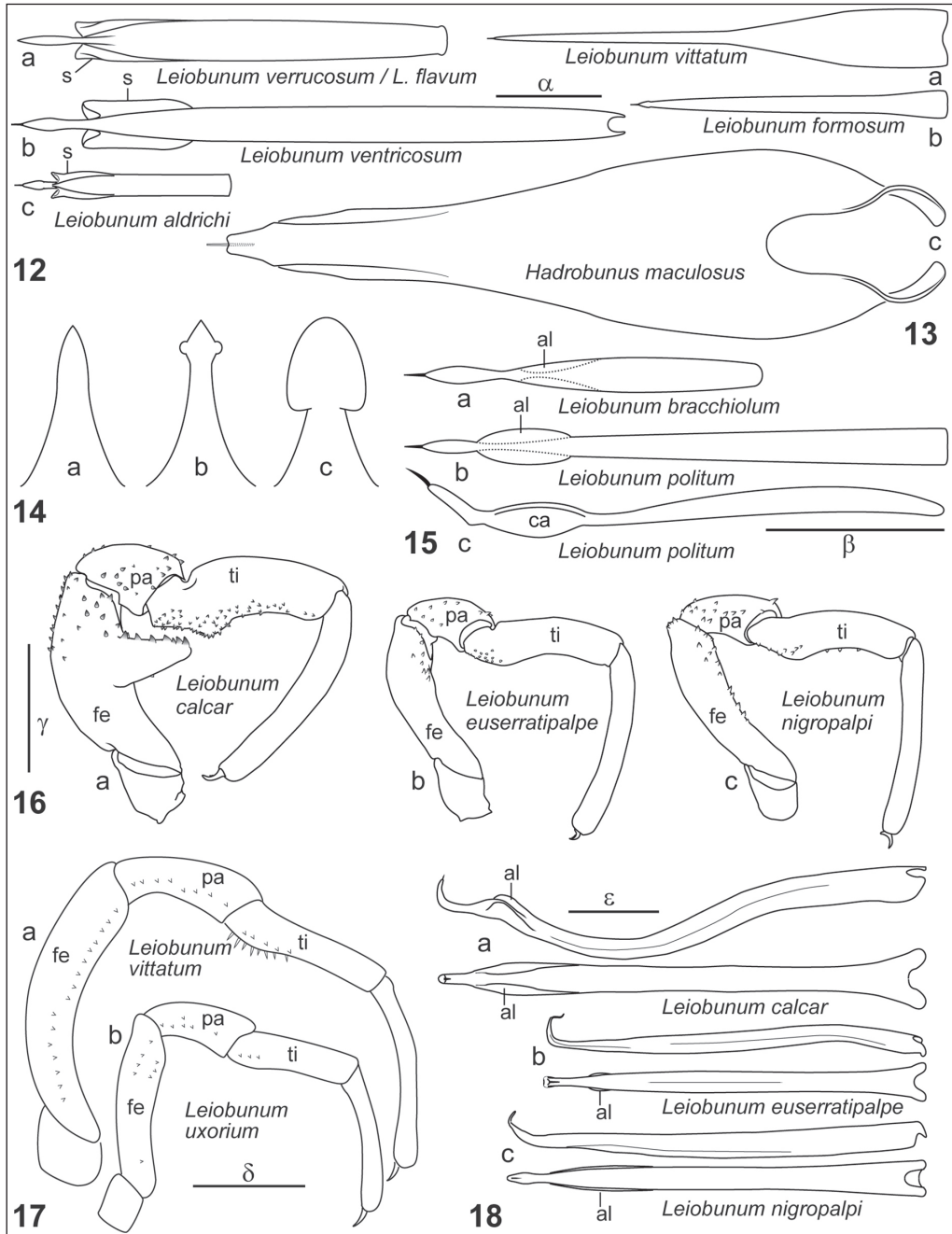
Figures 1–11 (previous page). External anatomy of harvestmen and key characters. Representative leiobunine harvestman: (1) Dorsal anatomy, palps, and legs removed at coxa-trochanter joint; (2) Ventral anatomy, left chelicera removed, palps removed at coxa-trochanter joint; (3) Right male palp (prolateral view). (4) Diversity of pedal claws (dorsal views). (5) Major patterns of dorsal sclerotization. (6) Representative penes (lateral views), showing difference between (a) phalangiids and (b–d) sclerosomatids. (7) *Caddo agilis*, right palp (prolateral view) only tubercular setae shown (after Shear 1974). (8) *Acropsopilio boopis*, as in Figure 7. (9) *Crosbycus dasyncnemus*, elongate palp and denticulate dorsum, scale bar = 1 mm. (10) *Hadrobunus maculosus*, female genital operculum, internal surface showing large anterior sclerite. (11) *H. maculosus*, male genital operculum, external surface, showing anterior median indentation. Abbreviations: ao = anal operculum, ca = carapace, cf = central figure, ch = chelicerae, cx = pedal coxa, exp = palpal coxa, dt = denticles (in row), et = eye tubercle (ocularium), fe = femur, ftg = free tergite, go = genital operculum, lr = labrum, mt = metapeltidium, oz = ozophore with opening to repugnatorial gland, pa = patella, rs = retrolateral spur II, sc = scutum, st = sternite, ta = tarsus, tb = setose tubercle, ti = tibia, tr = trochanter.

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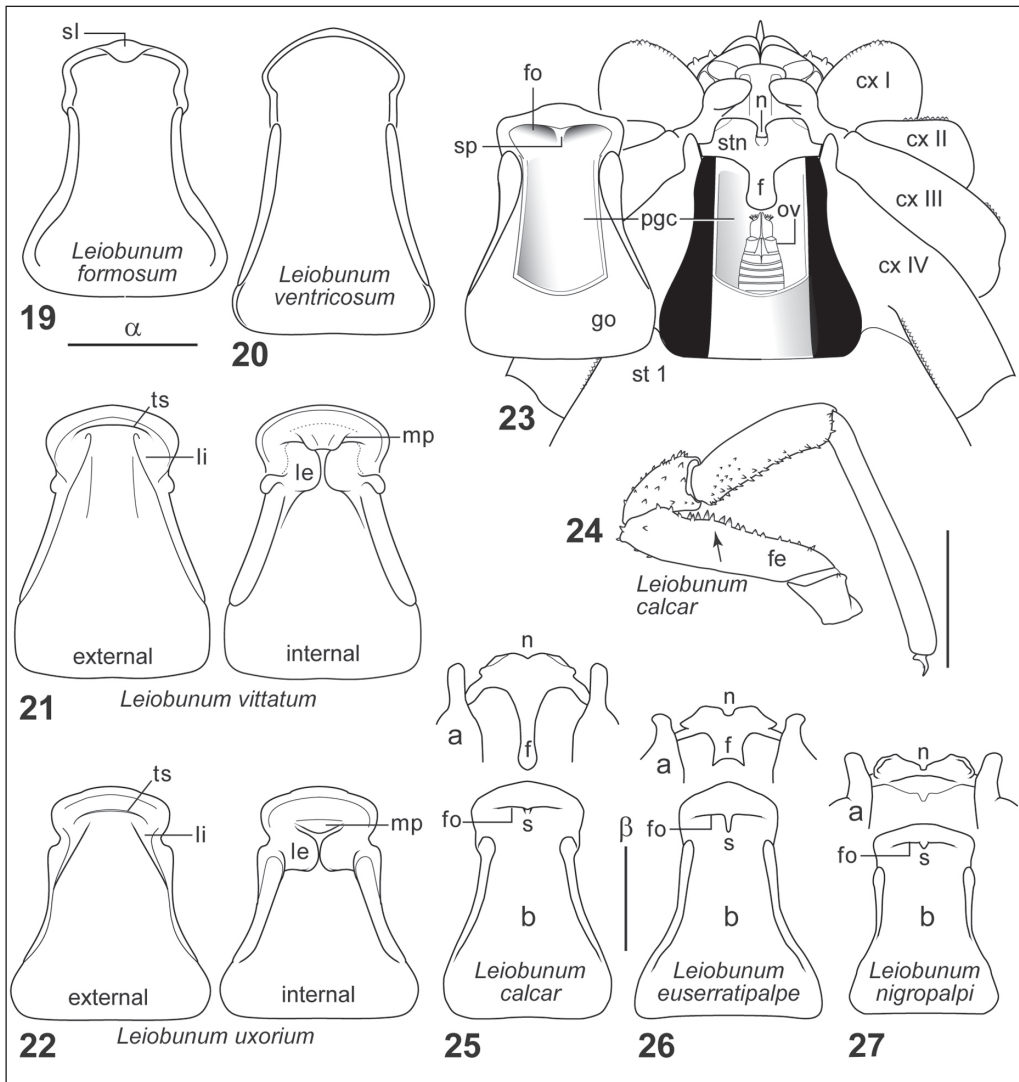
Figures 12–18 (following page). Key characters for male Leiobuninae. (12) Representative penes with subterminal sacs (s), dorsal views. (13) Representative penes without subterminal sacs, dorsal views. (14) Labrum diversity (lr; ventral views) (cf. Fig. 2). (15) Representative penes showing lateral alae (al) and vertical carina (ca): (a, b) dorsal view, (c) lateral view. (16) Male palps of *calcar* species-group, retrolateral views. (17) Male palps, *vittatum* species-group, retrolateral views. (18) Penes, *calcar* species-group, lateral views above dorsal views. Abbreviations: al = ala, ca = carina, fe = femur, pa = patella, s = sac, ti = tibia. All scale bars = 1 mm:  $\alpha$  for Figures 12–13;  $\beta$  for Figure 15a–c;  $\gamma$  for Figure 16a–c;  $\delta$  for Figure 17a,b;  $\epsilon$  for Figure 18a–c.

### Key to the Adult Harvestmen of Maryland

This key is designed for species-level identification of adult harvestmen found in Maryland but will likely identify immatures of those species resolved in couplets 1 through 6, which are distantly related and have very distinctive morphologies. The remaining species are more closely related, and juveniles of one species cannot

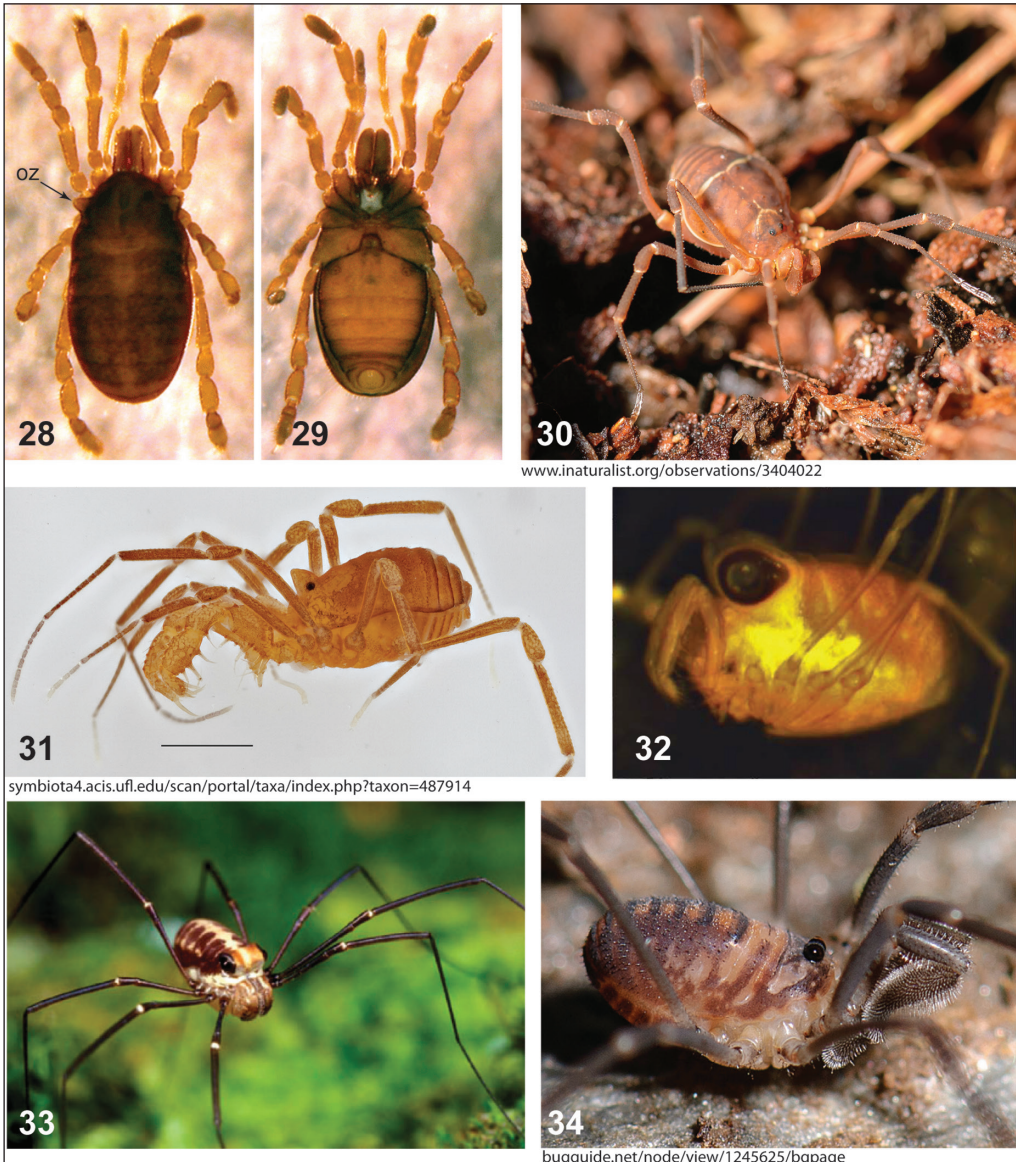


Figures 12–18. [Caption on previous page.]

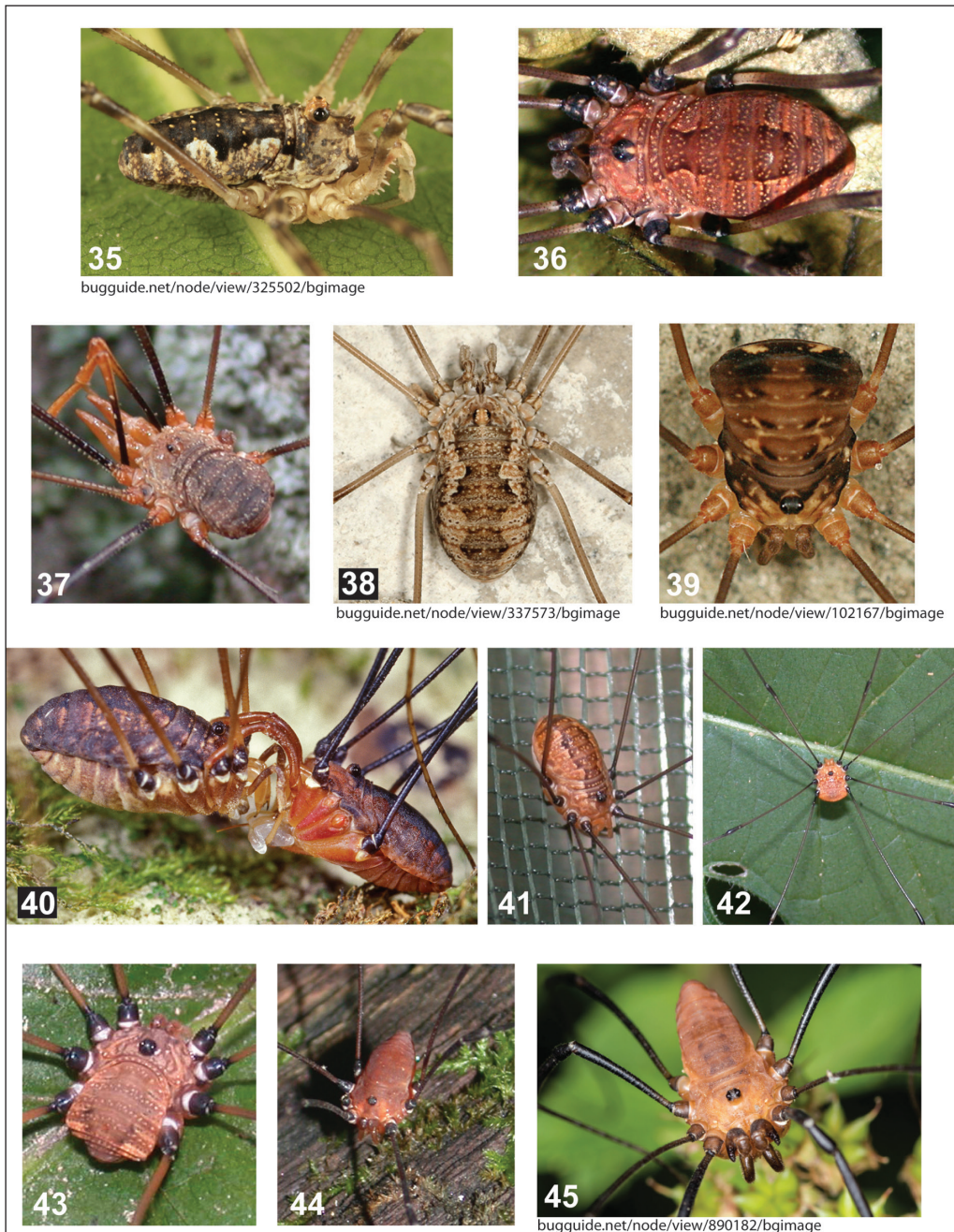


Figures 19–27. Key characters for female *Leioabunum*. (19) *L. formosum*, female genital operculum, internal view, showing anterior sclerotized lobe (sl). (20) *L. ventricosum*, internal, example of a simple genital operculum. (21) *L. vittatum*, genital operculum. (22) *L. uxorium*, genital operculum. (23) *Leioabunum hoffmani* Ingianni, McGhee, and Shultz (not found in Maryland), ventral surface with genital operculum cut away and flipped to show internal structures of the sterno-opercular mechanism in the *calcar* species-group (cf. Figs. 2, 25–27). (24) *L. calcar*, right palp, retrolateral view, showing low, denticulate apophysis. (25–27) Sterno-opercular mechanisms in the *calcar* species-group: (a) sternum (internal/ventral view), (b) genital operculum (internal/dorsal view) (cf. Fig. 23). Abbreviations: sl = anterior sclerotized lobe, cx = pedal coxa, f = sternal fultura, fe = femur, fo = transverse opercular fossa, go = genital operculum, le = lateral entapophysis, li = lateral indentation, mp = median phragma, n = median sternal notch, ov = ovipositor, pgc = pregenital chamber, sl = anterior sclerotized lobe, sp = median opercular septum, st 1 = first sternite, stn = sternum, ts = transverse sulcus. All scale bars = 1 mm:  $\alpha$  for Figures 19–22;  $\beta$  for Figures 25–27.

yet be reliably distinguished from those of others. Although interspecific differences among immatures are often substantial, developmental changes in color and structure have yet to be rigorously documented for any species. In general, juvenile phalangioids have very soft cuticles, relatively large eyes, sealed genital opercula, distoprolateral setose lobes (apophyses) on the palpal tibia and/or patella, and little to no cuticular armature (denticles, tubercles, spinules, etc.). The key uses many

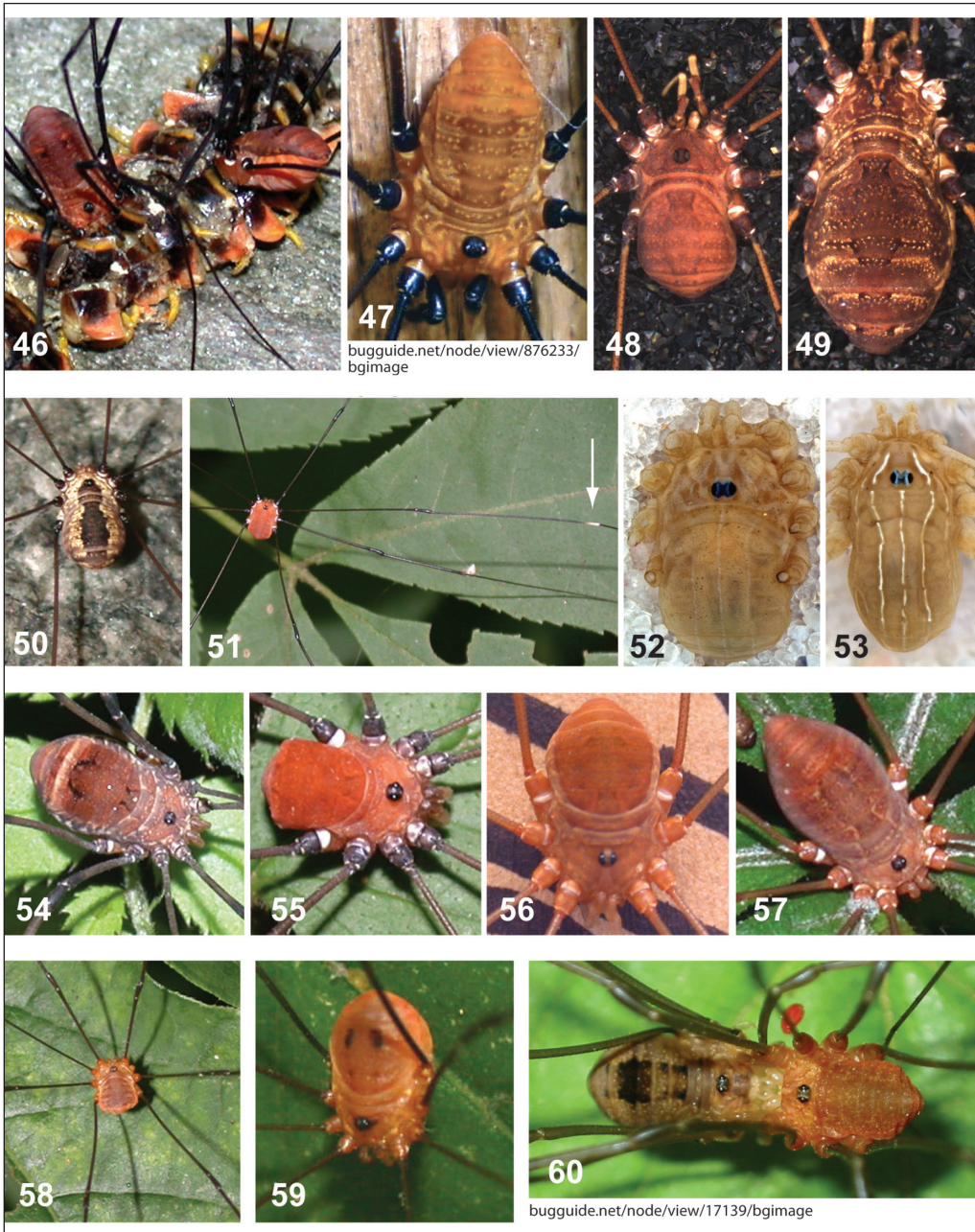


Figures 28–34. Representative harvestman species of Maryland. *Siro exilis*: (28) dorsal, (29) ventral. (30) *Vonones sayi* (© Marshal Hedin\*). 31, *Erebomaster acanthinus* (© Marshal Hedin\*\*). (32) *Acropsopilio boopis*. (33), *Caddo agilis* (© Joe Warfel). (34) *Sabacon cavicolens* (© Marshal Hedin). \*Creative Commons license (creativecommons.org/licenses/by/4.0/legalcode). \*\*Creative Commons license (creativecommons.org/publicdomain/zero/1.0/).



Figures 35–45. Representative harvestman species of Maryland. (35) *Odiellus pictus* (© Tom Murray\*). (36) *Hadrobunus maculosus*. (37) *Phalangium opilio*, male. (38) *P. opilio*, female (© Lynette Elliott\*). (39) *Nelima elegans* (© Tom Murray\*). (40) *Leiobunum vitatum*, mating, male on right (© Joe Warfel). (41) *L. uxorium*, female. (42) *L. uxorium*, male. (43) *L. euserratipalpe*, female. (44) *L. euserratipalpe*, male. (45) *L. calcar*, male (© John Rosenfeld). \*Creative Commons license (<https://creativecommons.org/licenses/by-nd-nc/1.0/>).





Figures 46–60. Representative *Leiobunum* species of Maryland. (46) *L. nigropalpi*, females feeding on polydesmid millipede. (47) *L. nigropalpi*, male (© Even Dankowicz\*). (48) *L. formosum*, male. (49) *L. formosum*, female. (50) *L. aldrichi*, female. (51) *L. aldrichi*, male, showing distal white band on tibia II. (52) *L. cretatum*, preserved adult. (53) *L. cretatum*, preserved subadult. (54) *L. verrucosum*, female. (55) *L. verrucosum*, male. (56) *L. flavum*, male. (57) *L. ventricosum*, female. (58) *L. bracchiolum*, male. (59) *L. bracchiolum*, female. (60) *L. politum*, mating, male on right (BradOfAnnArbor\*). \*Creative Commons license (<https://creativecommons.org/licenses/by-nd-nc/1.0/>).

new features discovered recently during taxonomic revisions (Ingianni et al. 2011), studies of mating-system evolution (Burns and Shultz 2015, Burns et al. 2013) and original work by the author.

- 1' Body length < 2 mm; dorsum with one consolidated sclerite (scutum completum; Figs. 5a, 28); eyes absent; opening to each defensive gland mounted on a prominent projection (ozophore [oz]; Figs. 5a, 28); pregenital chamber always open, not completely covered by genital operculum (Fig. 29); leg II not significantly longer and thinner than adjacent legs (Figs. 28, 29); Garrett County. [Cyphophthalmi: Sironoidea: Sironidae] ..... ***Siro exilis* Hoffman**
- 1'' Body length variable; dorsum without scutum completum; eyes present on median tubercle (Figs. 1, 5b–c, 9, 30–60); openings to defensive glands not so prominent (oz; Fig. 1); pregenital opening covered by posteriorly hinged genital operculum (go; Figs. 2, 23); leg II clearly longer and thinner than adjacent legs; widely distributed [Phalangida] ..... 2
- 2'(1'') Carapace and first 5 abdominal tergites fused to form a large plate (scutum magnum) (Figs. 5b, 30, 31); legs I and II each with 1 simple claw (Fig. 4a), legs III and IV each with either 2 claws (Fig. 4b) or 1 Y-shaped claw (Fig. 4c) [Laniatores] ..... 3
- 2'' Carapace not fused with abdominal scutum or tergites (Figs. 1, 5c), usually with last segment of carapace (metapeltidium) distinct (mt; Figs. 1, 5c) or reduced (Fig. 9); each leg with 1 simple claw (Fig. 4a) [Palpatores] ..... 4
- 3'(2') Body ~6 mm long; palpal tibia dorsoventrally flattened, concave ventrally, without large spines, held tightly against chelicerae in life (Fig. 30); eye tubercle low, wide; legs III and IV each with 2 claws (Fig. 4b); dorsum red-brown, often marked with light lines (Fig. 30) [Cosmetidae] ..... ***Vonones sayi* (Simon)**
- 3'' Body < 2 mm long; palpal tibia not dorsoventrally flattened, armed with long spines; eye tubercle elevated, conical (Fig. 31); leg III and IV each with a single Y-shaped claw, each branch with mid-ventral spur (Fig. 4c) (early immatures with terminal arolium and 3 pairs of small spurs); body yellow to light brown [Travuniidae] ..... ***Erebomaster acanthinus* (Crosby and Bishop)**
- 4'(2'') Body length < 1 mm (Fig. 9); palp thin, very long, about as long as leg I, without claw; legs with atypical wavy, interwoven setae; scutum with 3–5 fused tergites, dorsal sclerites with numerous small denticles [Dyspnoi: Ischyropsalidoidea: Taracidae] ..... ***Crosbycus dasyncnemus* (Crosby)**
- 4'' Body length 2–6 mm; palps robust with tibia and tarsus inflated, both with dense coat of erect setae; palpal tarsus capable of being flexed tightly against tibia; palpal tarsus lacking obvious claw; dorsum and dorsal

- sclerites without denticles (Fig. 34) [Dyspnoi: Ischyropsalidoidea: Sabaconidae] ..... ***Sabacon cavicolens* (Packard)**
- 4''' Body length, palps and dorsal armature variable, but not fitting preceding descriptions, palpal claw well developed (e.g., Fig. 3) ..... 5
- 5'(4''') Eyes and eye tubercle large, eye tubercle covering most of carapace (Figs. 32, 33); palpal femur with 3 or 4 large spine-like projections and one prominent distoprolateral setose tubercle (tb; Figs. 7, 8); males absent ..... 6
- 5'' Eyes and eye tubercle not so large; palpal femur variable but not as described above; males common [Eupnoi: Phalangioidae] ..... 7
- 6'(5') Body length ~3 mm (Fig. 33); palpal trochanter, patella, and tibia without large spine-like projections; palpal femur with 3 large ventral projections, about evenly spaced; palpal tarsus longer than tibia (Fig. 7) [Eupnoi: Caddoidea: Caddidae] ..... ***Caddo agilis* Banks**
- 6'' Body length < 1 mm (Fig. 32); palpal trochanter, patella, and tibia each with 1 or more large spine-like projections; palpal femur with 4 spine-like projections (2 proximal, 1 mid-femur, 1 distoproventral); palpal tarsus shorter than or subequal to tibia (Fig. 8) [Dyspnoi?: Acropsopilionidae] ..... ***Acropsopilio boopis* (Crosby)**
- 7'(5'') Palpal claw without ventral teeth; penis glans large, inflated; glans-shaft joint very well developed, glans capable of being acutely flexed dorsally against shaft (Fig. 6a) [Phalangiidae] ..... 8
- 7'' Palpal claw with ventral row of small, sharp teeth (Fig. 3); penis glans not greatly inflated relative to adjacent shaft, glans not capable of being acutely flexed dorsally against shaft (Figs. 6b–d, 12, 13, 15, 18) [Sclerosomatidae: Leiobuninae] ..... 9
- 8'(7') Anterior margin of carapace with 3 prominent spines (trident); palpal femur with retroventral row of 8–10 prominent projections, each with terminal seta; second cheliceral segment unmodified and palps not long and thin (Fig. 35); forests ..... ***Odiellus pictus* (Wood)**
- 8'' Anterior margin of carapace without prominent spines; palpal femur without retroventral row of prominent projections (Figs. 37, 38); male chelicerae with large, proximodorsal, cone-like projection on second article that normally projects anteriorly in life; male palps long and thin (Fig. 37); human-impacted habitats ..... ***Phalangium opilio* L.**
- 9'(7'') Body length variable; all pedal coxae with submarginal posterior and/or anterior rows of distinctive denticles (dt; Fig. 2) differing from armature present elsewhere on coxa; dorsal sclerites more or less hardened, sometimes armed with tubercles or denticles; pedal tarsi without alternating light and dark bands; dorsal coloration variable (Figs. 36, 40–60) but not as described below ..... 10

- 9" Body 5–8 mm long; pedal coxae III and IV without submarginal anterior and posterior rows of distinctive denticles (weakly developed anterior rows may occur on coxae I and II), all coxae with expansive field of scattered tubercles ending submarginally; dorsal cuticle flexible, unarmed except for low tubercles on eye tubercle; pedal tarsi with alternating light and dark bands; dorsum with variable bilateral pattern of white, brown and black markings, including prominent dark triangular marks posterolaterad to eye tubercle (Fig. 39) ..... *Nelima elegans* (Weed)
- 10'(9') Body length ~10 mm (Fig. 36); legs relatively short, femur I substantially shorter than length of body; scutum with numerous tiny, black, thorn-like, backward-curving denticles; male with broad median indentation at anterior margin of genital operculum (Fig. 11), scutum with 6 tergites, penis massive (Fig. 13c); female with large sclerite on inner anterior margin of genital operculum (Fig. 10) ..... *Hadrobunus maculosus* (Wood)
- 10" Body size variable; legs usually relatively longer, femur I subequal to or longer than body; scutum lacking tiny, black, thorn-like denticles; anterior margin of male genital operculum not indented (Fig. 2), male and female scutum usually with 5 tergites (Figs. 1, 5c); inner anterior margin of female genital operculum without large sclerite (Figs. 20–23, 25–27), although small sclerite occurs in female *Leiobunum formosum* (Fig. 19) [*Leiobunum*] ..... 11
- 11'(10") Male: palpal tarsus with proventral row of denticles (dt; Fig. 3); pregenital chamber enclosing unsegmented penis (Figs. 6b–d, 12, 13, 15, 18) ..... 12
- 11" Female: palpal tarsus lacking proventral row of denticles; pregenital chamber enclosing segmented ovipositor with terminal pair of finger-like processes, each bearing a sensory organ (ov; Fig. 23)..... 23

### Male *Leiobunum*

- 12'(11') Penis with subterminal pair of cuticular sacs with anterior openings (s; Figs. 6d, 12a–c), contents (nuptial gift) often present; labrum not greatly inflated distally (Fig. 14a, b); pedal trochanters may or may not be concolorous with base color of dorsum ..... 14
- 12" Penis (Fig. 15) without sacs but with subterminal vertical carina (ca) ventrally and transverse alae (al) dorsally, thus roughly T-shaped in cross section creating a pair of lateral concavities often containing oval mass (nuptial gift); tip of labrum greatly inflated (Fig. 14c); pedal trochanters concolorous with base color of dorsum ..... 13
- 12''' Penis without subterminal sacs or T-shaped region (Figs. 6b–c, 13a–b), but small, solid lateral alae may be present (al; Fig. 18); labrum not greatly inflated distally (Fig. 14a, b); pedal trochanters may or may not be concolorous with base color of dorsum ..... 18

- 13'(12") Body length ~4 mm (Fig. 60); penis > 2.5 mm long, subterminal dorsal alae extending laterad beyond proximally adjacent shaft (Fig. 15b) .....  
***Leiobunum politum* (Wood)**
- 13" Body length ~3 mm (Fig. 58); penis < 2 mm long, with subterminal alae not extending laterad beyond proximally adjacent shaft (Fig. 15a) .....  
***Leiobunum brachiolum* McGhee**
- 14'(12') Labrum with subterminal pair of small tubercles, tip may resemble an arrowhead (Fig. 14b) ..... 15
- 14" Labrum tapering to point, without subterminal pair of tubercles (Fig. 14a) ..... 16
- 15'(14') Pedal trochanters dark, contrasting with dorsum and coxae; dorsum of mature adult predominately red-brown with dark anterior and posterior remnants of central figure (Fig. 55); however, dorsum variable in young adults (April–May) similar to that of early-season females, with light red-brown base color, prominent dark central figure, and transverse bands of light flecks on abdomen or gradations between this and mature coloration .....  
***Leiobunum verrucosum* (Wood)**
- 15" Pedal trochanters and dorsum light to golden brown, contrasting slightly with coxae (Fig. 56); trace of a long, thin central figure sometimes present early in season (April–May) .....  
***Leiobunum flavum* Banks**
- 16'(14") Body 7–8 mm long, abdomen extended, pointed posteriorly; dorsum and trochanters light to golden brown (as in Fig. 57); central figure usually present on scutum, usually extending forward to just behind eye tubercle, slightly darker than rest of dorsum, outlined in white, at least anteriorly; central figure sometimes faded or obsolete .....  
***Leiobunum ventricosum* (Wood)**
- 16" Body < 5 mm long, abdomen rounded or truncated posteriorly (e.g., Figs. 1, 2, 51, 52); coloration not as above ..... 17
- 17'(16") Tibia of leg II with broad distal white band (Fig. 51) (femora and tibiae of other legs may have narrow distal white bands, especially in early summer); pedal trochanters dark, contrasting with lighter coxae; dorsum predominantly orange to orange-brown, central figure present to absent but lacking 5 fine, longitudinal white lines .....  
***Leiobunum aldrichi* Weed**
- 17" Tibiae of all legs without white distal band, often darkening distad; dorsum ranging from yellow to brown, pedal trochanters concolorous with dorsum, not contrasting significantly with coxae (Fig. 52); dorsum without central figure but with up to 5 fine, longitudinal white lines (1 median, 2 paramedian, 2 lateral) (Fig. 52), lines more prominent in subadults (Fig. 53) .....  
***Leiobunum cretatum* Crosby and Bishop**
- 18'(12"") Penis tapering gradually towards tip in dorsal view (Fig. 13b), distal four-fifths of shaft compressed dorsoventrally and basal one-fifth expanding

proximal in lateral view (Fig. 6c); usually with small, conical spike on coxa II just mediad to posterior articulation with trochanter (Fig. 1: rs)  
..... ***Leiobunum formosum auct. sensu Davis***

- 18" Not fitting previous description ..... 19
- 19'(18") Proximal one-half to one-third of penis broad in dorsal view (Fig. 13a), thickened in lateral view (Fig. 6b), distal one-half to two-thirds of penis narrow; shaft without alae [*vittatum* species-group] ..... 20
- 19" Penis parallel-sided to tapering distad; shaft usually with subterminal alae, though sometimes small (Fig. 18) [*calcar* species-group] ..... 21
- 20'(19") Body length ~6 mm; palpal femur (Figs. 17a, 40) strongly curved, long (distal end of fully-levated femur extending to a point far above dorsal surface of eye tubercle); proximoventral surface of tibia more or less inflated, proximoventral half of tibia armed with long spine-like denticles; penis > 3 mm long; abdomen usually extended posterior to scutum (Fig. 40) ..... ***Leiobunum vittatum* (Say)**
- 20" Body length ~4 mm; palpal femur (Fig. 17b) only slightly curved, not as long (distal end of fully levated femur extending to a point even with or slightly above the dorsal surface of the eye tubercle); proximoventral surface of tibia not inflated, proximoventral half of tibia essentially unarmed, spine-like denticles absent; penis < 3 mm long; abdomen truncated posteriorly (Fig. 42) ..... ***Leiobunum uxorium Crosby and Bishop***
- 21(19") Palpal femur (Fig. 16a) inflated, with prominent but variably developed retrolateral, denticulate apophysis; proximoventral portion of palpal tibia enlarged, flattened, denticulate; penis (Fig. 18a) with broad ventral arch in lateral view, subterminal alae typically evident (folding dorsad) and associated with slight dorsal arch in shaft ..... ***Leiobunum calcar* (Wood)**
- 21" Palpal femur (Figs. 16b,c) not significantly inflated, without prominent retrolateral apophysis; proximoventral portion of palpal tibia not modified as above; penis shaft (Fig. 18b,c) essentially straight, subterminal alae less evident, not associated with dorsal arch in shaft ..... 22
- 22'(21") Retrolateral denticles of palpal femur restricted to distal third, some arranged in subterminal cluster; proximoventral surface of tibia slightly inflated, denticulate (Fig. 16b); penis (Fig. 18b) without clear glans-shaft joint, shaft slightly curved in lateral view; paired subterminal alae short; palpal femur, patella and proximal tibia not black (Fig. 44) ..... ***Leiobunum euserratipalpe Ingianni, McGhee and Shultz***
- 22" Retrolateral denticles of palpal femur not restricted to distal third, not arranged in retrolateral cluster; proximoventral surface of tibia with robust, often-angular projection (Fig. 16c); glans-shaft joint of penis evident in dorsal or ventral perspective as constriction; shaft essentially straight in lateral view; paired subterminal alae weakly developed, long,

narrow (Fig. 18c); palpal femur, patella and proximal tibia usually black (Fig. 47) ..... *Leiobunum nigropalpi* (Wood)

### Female *Leiobunum*

- 23'(11") Inner anterior margin of genital operculum with median sclerotized lobe (Fig 19: sl), a continuation of the external cuticle into flexible cuticle of pregenital chamber, sometimes with enhanced sclerotization; coxa II with small conical spike just medial to posterior articulation with trochanter (Fig. 1: rs); legs typically with 2 broad, dark bands: proximal band encompassing distal femur, patella and proximal tibia, distal band encompassing distal tibia and proximal basitarsus ..... *Leiobunum formosum* auct. *sensu* Davis (Fig. 49)
- 23" Inner anterior margin of genital operculum lacking median sclerotized lobe (Figs. 20–23, 25–27); coxa II usually without conical spike medial to posterior articulation with trochanter, although low tubercle or denticle may be present; leg banding other than above or absent ..... 24
- 24'(23") Anterior part of genital operculum externally with deep transverse sulcus (ts; Figs. 21, 22) corresponding internally to transverse median phragma (mp; Figs. 21, 22), also externally with anterolateral indentations (li; Figs. 21, 22) corresponding internally to 2 large lateral entapophyses, entapophyses touching or nearly touching medially (le; Figs. 21, 22) [*vittatum* species-group] ..... 25
- 24" Genital operculum without deep transverse sulcus bilateral indentation or corresponding internal structures ..... 26
- 25'(24') Anterior external surface of genital operculum (Fig. 21) produced ventrally with transverse sulcus (ts) opening anteriorly, median phragma (mp) projecting posteriad over lateral entapophyses (le), phragma with shallow median trough; body ~8 mm long; coloration highly variable in time and place ..... *Leiobunum vittatum* (Say)
- 25" Anterior external surface of genital operculum (Fig. 22) nearly flat with transverse sulcus (ts) opening ventrally, median phragma (mp) not extending posteriad over lateral entapophyses (le) and lacking median trough; body ~6 mm long; coloration laterad to dark central figure usually golden-brown with light spots (Fig. 41) ..... *Leiobunum uxorium* Crosby and Bishop
- 26'(24") Sternum with median notch on free margin (n; Figs. 23, 25–27); genital operculum internally with anterior transverse fossa (fo) divided by median septum (s) [*calcar* species-group] ..... 27
- 26" Sternum without median notch on free margin; anterior part of genital operculum unspecialized (Fig. 20) ..... 29
- 27'(26') Palpal femur with low apophysis near mid-retroventral surface armed with large, sharp denticles (Fig. 24); sternum with median sclerotized

fultura (f; Fig. 25a) projecting posteriorly within otherwise flexible cuticle of pregenital chamber, fultura longer than half width of sternum .....

***Leiobunum calcar* (Wood)**

- 27" Palpal femur without retrolateral apophysis; sternal fultura (f) subequal to or shorter than width of sternum (Fig. 26a) or absent (Fig. 27a) ..... 28
- 28'(27") Sternum without median fultura projecting posteriorly into flexible cuticle of pregenital chamber (Fig. 27a), although region posterior to sternum may be stiffer than surrounding cuticle; base color of dorsum yellow- to red-brown with dark central figure variably broken and crossed by transverse rows of light and dark spots (e.g., Fig. 46)..... ***Leiobunum nigropalpi* (Wood)**
- 28" Sternum with median fultura projecting posteriorly into flexible cuticle of pregenital chamber, length of fultura less than width of sternum (Fig. 26a); coloration of dorsum highly variable; base color of brown, dark central figure present to absent, usually darkest near posterior end of scutum; when present, central figure may be crossed by transverse rows of light spots (e.g., Fig. 43), sometimes central figure absent and dorsum a near-uniform brown ..... ***Leiobunum euserratipalpe* Ingianni, McGhee, and Shultz**
- 29'(26") Dorsum predominately dark brown; scutum with evident remnants of dark central figure and scutum typically ending in light transverse belt; trochanters dark, contrasting strongly with coxae (Fig. 54); however, dorsum variable in young adults (April–May) similar to that of early-season males, with light red-brown base color, prominent dark central figure, and transverse bands of light flecks on abdomen or gradations between this and mature coloration ..... ***Leiobunum verrucosum* (Wood)**
- 29" Not fitting previous description ..... 30
- 30'(29") Dorsum and pedal trochanters a nearly uniform shade of light to golden brown, except for central figure (Figs. 56, 57); body > 8 mm long ..... 31
- 30" Dorsum and pedal trochanters otherwise; body < 6 mm long ..... 32
- 31'(30') Body 8–10 mm long; central figure absent or expressed as medial pair of dark marks on anterior and posterior ends of scutum (as in Fig. 56), although early adults (April–May) may have a brown central figure fading with age to mature condition above; abdomen usually bluntly rounded posteriorly ..... ***Leiobunum flavum* Banks**
- 31" Body 10–12 mm long; central figure usually beginning behind eye tubercle and extending to end of scutum, slightly darker than rest of dorsum, outlined in white, at least anteriorly; central figure sometimes faded or obsolete; abdomen extended posteriorly, narrowing to blunt point (Fig. 57) ..... ***Leiobunum ventricosum* (Wood)**



- 32'(30") Tibia II with broad distal white band (as in Fig. 51) (femora and tibiae of other legs may have narrow distal white bands, especially in early summer); scutum with dark central figure (Fig. 50) potentially extending from eye tubercle posteriorly to anal operculum but usually abbreviated to varying lengths posteriorly; abdomen with segmental bands of irregular light spots, base color of dorsum variable; pedal trochanters dark, contrasting with coxae and base color of dorsum ..... ***Leiobunum aldrichi* Weed**
- 32" Tibia II without broad white band, dorsal coloration variable, pedal trochanters concolorous with base color of dorsum ..... 33
- 33'(32") Dorsum ranging from yellow to brown, without central figure but with up to 5 fine, longitudinal white lines (1 median, 2 paramedian, 2 lateral) (Fig. 52), lines more prominent in subadults (Fig. 53); pedal trochanters concolorous with dorsum, not contrasting significantly with coxae; pedal tibiae often darkening distad ..... ***Leiobunum cretatum* Crosby and Bishop**
- 33" Dorsum without thin longitudinal lines ..... 34
- 34'(33") Dark central figure potentially extending continuously from anterior margin of carapace to last tergite, but often reduced or enhanced along its path (Fig. 60); otherwise base color of dorsum usually a shade of red-brown and/or purple; abdominal dorsum with transverse segmental bands of irregular light spots; pedal trochanters concolorous with base color of dorsum; body ~6 mm long ..... ***Leiobunum politum* (Wood)**
- 34" Dark central figure restricted to abdominal scutum, where it may be present, reduced or absent, often represented by one or more pairs of dark spots (Fig. 59); dorsum and pedal trochanters predominately yellow, yellow-brown or yellow-orange; body ~5 mm long ..... ***Leiobunum brachiolum* McGhee**

### Diagnosis and Summary of Species Known or Expected to Occur in Maryland

***Acropsopilio boopis* (Crosby).** Not yet recorded from Maryland. *Diagnosis:* Very small (body ~1 mm long); eyes and eye tubercle very large, eye tubercle covering most of carapace (Fig. 32); palpal trochanter through tibia armed with 1 or more spine-like projections, 4 on femur (2 proximal, 1 midfemur, 1 distal) (Fig. 8); length of palpal tarsus less than or subequal to that of tibia; only females known (see Shear 1974 for details). *Distribution:* Scant records from Ontario, Quebec, New England, the Great Lakes Region (Cokendolpher and Lee 1993) and, recently, mountains of North Carolina (Shultz 2013), also Japan; expected in mountainous western part of Maryland. Shear (1974) notes that specimens are usually found by sifting or Berlese extraction of *Sphagnum* or leaf litter obtained from moist areas, often near bodies of water. *Note:* Although *Acropsopilio* is traditionally placed in the Eupnoi with *Caddo* (which it strongly resembles) and with the Phalangioidea,

a recent molecular phylogenetic study (Groh and Giribet 2015) suggests that *Acropsopilio* belongs in Dyspnoi, with *Sabacon* and *Crosbycus*. *Common synonym: Caddo boöpis* Crosby.

***Caddo agilis* Banks.** *Diagnosis:* Small (body ~3 mm long); legs long, thin; eye and eye tubercle very large, eye tubercle occupying most of carapace (Fig. 33); palpal femur with prodistal setose tubercle and 3 ventral spine-like projections, about evenly spaced (Fig. 7), no spine-like projections on other palpal segments; carapace silvery white (opalescent) laterally; eye tubercle with white median stripe; abdominal dorsum purple-brown with white median line crossed by segmentally arranged, white transverse lines; known almost exclusively from females (see Shear 1974 for details). *Distribution:* Forests of northeastern US and southeastern Canada west to Wisconsin, increasingly limited to the Appalachian Mountains in southern states (Virginia, Tennessee, North Carolina) (Shultz 2013), also Japan and adjacent Kuril Islands. In Maryland, known from Gambriel State Park (Frederick County) and from forest surveys by the Maryland Department of Natural Resources in Garrett County (J.W. Shultz, pers. observ.); likely to occur throughout mountainous western and possibly some northern counties. This is the first published record of the species in Maryland, but its occurrence was expected given its presence in Pennsylvania, Virginia, and West Virginia (Cokendolpher and Lee 1993). The species moves actively over surfaces in forests in early summer.

***Crosbycus dasycnemus* (Crosby).** Not yet recorded from Maryland. *Diagnosis:* Very small (body  $\leq 1$  mm long), palp extremely long, thin, (subequal to leg 1), patella very long, tarsus without claw (Fig. 9); eye tubercle positioned near anterior margin of carapace; carapace, *scutum parvum*, free tergites and anal operculum usually dark, armed with numerous denticles (unincorporated scutal tergites may occur in immatures); pedal femur, patella and tibia with unusual setae (erect then bending distad and running parallel to leg surface, sinuate, interwoven); known only from females in North America, but some males known from Japan (Tsurusaki 1993). *Distribution:* Southeastern Canada and eastern, Midwestern, and Appalachian regions in the US. (Cokendolpher and Lee 1993, Shear 1986), also Japan and eastern China (Tsurusaki 1993). Collected mostly (but rarely) from deciduous leaf litter and moss, most commonly via Berlese funnels or pitfalls (Shear 1986). The species is known from Pennsylvania, Virginia, and West Virginia (Cokendolpher and Lee 1993) and is thus expected in Maryland.

***Erebomaster acanthinus* (Crosby and Bishop).** *Diagnosis:* Small (body  $\leq 2$  mm long), dorsum with scutum magnum and 3 free tergites (Figs. 5b, 31); eye tubercle prominent, conical; palpal segments robust, spiny; 1 simple claw on legs I and II (Fig. 4a), 1 Y-shaped claw on legs III and IV, with small ventral spur on each claw branch (Fig. 4c) (early immatures with terminal arolium and 3 pairs of small lateral spurs); color yellow to orange (see Briggs 1969 for details). *Distribution:* District of Columbia, Maryland, North Carolina, Virginia, West Virginia, and eastern Kentucky. Known from Maryland west of Chesapeake Bay in leaf litter, under logs, etc. in deciduous forests; recorded from Garrett, Montgomery, Prince Georges, and Anne Arundel counties (Muma 1945a, b; J.W. Shultz, pers.

observ.); no records from Delmarva. *Note*: Variation in *E. acanthinus* and relatives suggests that there is greater taxonomic diversity in the genus than currently recognized. Absence of ventral spurs on claws of legs III and IV is characteristic of *E. flavescens*, but it is unclear whether the range of this species, which apparently extends into New York (Bishop 1949), encompasses any part of Maryland. *Common synonyms*: *Phalangodes acanthina* Crosby and Bishop, *Erebomaster acanthina* (Crosby and Bishop)

***Hadrobunus maculosus* (Wood)**. *Diagnosis*: Robust (Fig. 36), body length ~10 mm; scutum with numerous tiny, black, thorn-like denticles; legs relatively short (femur I shorter than body). Male: Abdomen with 6 scutal tergites, 2 free tergites; anterior margin of genital operculum with broad median indentation (Fig. 11); heavily sclerotized sternum and labium; massive penis (Fig. 13c). Female: Genital operculum with large sclerite on inner anterior margin (Fig. 10); heavily sclerotized sternum. *Distribution*: Atlantic Seaboard from North Carolina to New Hampshire (northern limit uncertain), western limit within central New York, western Pennsylvania, eastern West Virginia, western Virginia, western North Carolina. Found throughout Maryland west of Chesapeake Bay; no records from Delmarva. Open or broken woodlands and adjacent non-wooded areas, including agricultural fields; less abundant in mature forests. Adults largely nocturnal, found under loose objects on the ground during the day. Mid-Atlantic populations mistakenly called *H. grandis* (Say) in most previous literature (Shultz 2012).

***Leiobunum aldrichi* Weed**. *Diagnosis*: Both sexes with broad, terminal white band on tibia II (Fig. 51) (narrow terminal bands possible on femora and tibia of other legs, especially in subadults and young adults); eye tubercle and pedal trochanters dark. Male (Fig. 51): Body 3–4 mm long; legs extremely long (Fig. 51); body coloration variable but often orange-brown, central figure present to absent; penis short with bilateral pair of sacs (s; Fig. 12c); labrum ends in simple point (Fig. 14a). Female (Fig. 50): Body 4.5–6 mm long; dark central figure potentially extending from eye tubercle to anal operculum (Fig. 50) but often abbreviated posteriad to varying degrees, interrupted by transverse rows of light flecks and spots that extend from lateral portions of abdomen; ground color brown to orange. *Distribution*: Woodlands throughout eastern North America, from Atlantic Coast to Great Plains; report from British Columbia (Bishop 1949) requires confirmation. Most common in relatively undisturbed forests, but often absent in seemingly suitable post-agricultural woodland (J.W. Shultz, pers. observ.). Often observed on tree trunks, boulders and other surfaces; may occur locally in large numbers; will spiral upward on tree trunks like a squirrel to escape. Aspects of the biology of *L. aldrichi* in Michigan can be found in Edgar (1971; as *L. longipes*). *Common synonyms*: *Leiobunum longipes* Weed, *L. gordonii* Goodnight and Goodnight

***Leiobunum brachiolium* McGhee**. *Diagnosis*: Male (Fig. 58): Body ~3 mm long, dorsum and pedal trochanters yellow to reddish orange; labrum greatly inflated (as in *L. politum*) (Fig. 14c); penis < 2 mm long (Fig. 15a), subterminal region of shaft with ventral vertical carina and dorsal transverse alae (thus, somewhat T-shaped in cross section, as in *L. politum*), but alae not extending laterad beyond proximally

adjacent shaft. lateral cavities formed by T-shaped apparatus often containing oval-shaped mass of white material (nuptial gift) (as in *L. politum*). Female (Fig. 59): Body ~4.75 mm; color of dorsum varying from yellow to orange to yellow-brown, pedal trochanters concolorous with dorsum; central figure highly variable but restricted to scutum when present, ranges from solid to bilateral pairs of dark spots (Fig. 59) to absent. *Distribution*: Known from Appalachians and Atlantic and Gulf Coastal Plains of the US, western limit unclear due to persistent confusion with *L. politum* and inadequate taxonomic treatment of western members of the group; populations with penes like that of *L. brachiolum* occur in Minnesota (Shoemaker et al. 2017). In Maryland, *L. brachiolum* prefers herbaceous vegetation and leafy shrubs adjacent to or within wooded areas, not usually found moving across the forest floor as does *L. politum*. The 2 species commonly occur together at forest edges. The type locality for *L. brachiolum* is Crow's Nest Lodge near Thurmont, Frederick County, MD (McGhee 1975).

***Leiobunum calcar* (Wood).** *Diagnosis*: Male (Fig. 45): Body 6–7 mm long; palpal femur (Fig. 16a) inflated, with subterminal, retrolateral apophysis with denticulate distal margin (apophysis variably developed, small to large); proximoventral surface of tibia expanded, flattened, denticulate; ventral surface of palpal tibia concave, with long, erect setae. Penis long (Fig. 18a), shaft arching ventrally in lateral view, with bilateral pair of subterminal alae, alate region associated with slight dorsal arch in shaft, glans-shaft joint indistinct dorsally, glans curving dorsad, then posteriad. Posterior margins of genital operculum usually indistinct, fused with sternite 1. Abdomen extended posterior to scutum, often pointed. Female: Body 7–9 mm; palpal femur with low but distinct, retrolateral denticulate apophysis (Fig. 24); sternum with posterior median fultura embedded in soft cuticle of pregenital chamber (Fig. 25a), longer than half transverse width of sternum; as in all members of the *calcar* species-group (*L. euserratipalpe*, *L. nigropalpi*) sternum with distinct median notch at free margin (Fig. 25a); anterior inner surface of genital operculum modified to engage free margin of sternum (Fig. 25b, cf. Fig. 23). Dorsal coloration highly variable, yellow-brown to dark brown, central figure dark but varying from distinct to absent; may have transverse bands of spots. *Range*: Central to eastern North America, most widespread in northern part of range increasingly limited to mountains farther south. Known from Frederick and Garrett counties in Maryland, probably occurs throughout forests in mountainous west (see Ingianni et al. 2011 for details). Aspects of the biology of *L. calcar* in Michigan can be found in Edgar (1971).

***Leiobunum cretatum* Crosby and Bishop.** Not yet recorded from Maryland. *Diagnosis*: Small, males 2.3–3.5 mm long, females 2.6–5.25 mm long (Coken-dopher and Rapp 1985); legs very long; dorsum and pedal trochanters yellow to brown. Dorsum with up to 5 fine, longitudinal white lines, each extending anteriorly from the posterior end of the abdomen (Figs. 52, 53); that is, 1 median line ending at the eye tubercle, 2 paramedian lines extending to anterior margin of carapace (taking a wide berth around the eye tubercle), and 2 lateral lines passing forward to the level of coxa II; lateral lines sometimes reduced; lines much more prominent in

subadults (Fig. 53). Free abdominal tergites often with scattered rearward-slanting acuminate denticles. Penis short with pair of lateral sacs. *Range*: Central to eastern US, but with relatively few records. Not known from Maryland, but recorded from Pennsylvania and Virginia (e.g., near Great Falls on Potomac River; Cokendolpher and Lee 1993); occurs in deciduous woods (Cokendolpher and Rapp 1985). *Synonym*: *L. lineatum* Edgar.

***Leiobunum euserratipalpe* Ingianni, McGhee, and Shultz.** *Diagnosis*: Male (Fig. 44): Body ~6 mm long; palpal femur with subterminal, retrolateral cluster of denticles (Fig. 16b), retrolateral denticles not extending into proximal two-thirds of femur; proximoventral surface of palpal tibia slightly inflated, denticulate. Penis shaft nearly straight (Fig. 18b), subterminal pair of small lateral alae present; glans-shaft joint indistinct dorsally, glans curving dorsad, then posteriad. Dorsum yellow- to red-brown, central figure usually absent or expressed only on first scutal tergite; color of pedal trochanters variable. Female (Fig. 43): Palpal femur lacking denticulate apophysis of female *L. calcar* (see Fig. 24); sternum with posterior median fultura (f) embedded in soft cuticle of pregenital chamber (Fig. 26a), subequal to or shorter than half transverse width of sternum; free margin of sternum with median notch (n; Fig. 26a). As in *L. calcar* and *L. nigropalpi*: anterior inner surface of genital operculum modified to engage free margin of sternum (Fig. 26b, cf. Fig. 23), a transverse fossa (f) divided by small median septum (s); coloration highly variable, from that shown in Fig. 43 to near-uniform brown; central figure highly variable, well developed to absent, often more well-developed at posterior end of scutum. *Distribution*: Widespread in the eastern US, especially common along Atlantic Seaboard from coastal plain to high Piedmont, less common in mature forests. Very common early-to-midsummer species in Maryland, prefers bushy vegetation, forest edges and woodland with significant understory (see Ingianni et al. 2011 for details). *Common synonym*: *L. serratipalpe* auct. *sensu* Davis, not Roewer (= female *L. calcar*) (Cokendolpher 1981).

***Leiobunum flavum* Banks.** *Diagnosis*: Male (Fig. 56) 5.5–6.5 mm long, female body 8–10 mm long; dorsum of both sexes predominantly light to golden brown with traces of dark central figure on first and last scutal tergites, more prominent on female; early-season (May–June) individuals may have a long, narrow central figure, fading with age; pedal trochanters concolorous with dorsum; abdomen truncated to bluntly rounded posteriorly. As in *L. verrucosum*, male labrum with subterminal pair of lateral tubercles, giving arrowhead-like appearance to tip (Fig. 14b), and penis with subterminal pair of sacs (Fig. 12a). *Distribution*: From Atlantic Seaboard west to Great Plains and south to Texas, although above diagnosis will not accommodate many populations west of Mississippi River (probably a different species). Occurs in and near wooded areas; relatively few records from Maryland (Prince Georges and Anne Arundel counties; J.W. Shultz, pers. observ.), but probably widespread.

***Leiobunum formosum* auct. sensu** Davis, not Wood (= juvenile *L. verrucosum*). *Diagnosis*: Legs of both sexes typically with 2 broad, dark bands: proximal band encompassing distal femur, patella and proximal tibia, distal band

encompassing distal tibia and proximal basitarsus; with small, conical spike on coxa II just mediad to posterior articulation with trochanter (rs; Fig. 1) (also in *H. maculosus*), although denticle or low tubercle may be present in other species. Male (Fig. 48): Body ~6 mm long; penis without subterminal sacs, shaft tapering gradually distad in dorsal view (Fig. 13b), distal four-fifths of shaft dorsoventrally compressed, proximal one-fifth expanding proximad in lateral view (Fig. 6c); labrum ending in simple point (Fig. 14a). Dorsum of mature male red-brown with transverse bands of light spots, traces of central figure on anterior and posterior ends of scutum, superficially similar to male *L. verrucosum* (cf. Fig. 55); early season males with lighter dorsum and contrasting central figure. Female (Fig. 49): Body 9–10 mm long; anterior margin of genital operculum internally with median cuticular lobe (Fig. 19), a continuation of surface cuticle into soft floor of pregenital chamber, may have enhanced sclerotization. Mature female brown with transverse rows of light spots, central figure reduced but evident; color of early season females similar to early season males. *Distribution*: Ranging widely but discontinuously across eastern US from Gulf Coast north into Illinois, Indiana, and Ohio; known thus far in Maryland only from Delmarva (Worcester County). *Note*: The species is likely to be transferred to *Hadrobunus* in the near future (Burns et al. 2012). Also, juveniles of *L. verrucosum* correspond to Wood's (1868) original description of *L. formosum*, thus explaining Muma's (1945b) report of *L. formosum* in central Maryland. Aspects of the biology of *L. formosum* in southeastern Virginia can be found in Townsend et al. (2006).

***Leiobunum nigropalpi* (Wood).** *Diagnosis*: Male (Fig. 47): Body 5–6 mm long; palpal femur, patella and tibia dark brown to black, tarsus (and sometimes distal tibia) lighter; palpal femur with retrolateral denticles extending proximad to distal third of segment (Fig. 16c), without subterminal cluster of denticles or denticulate apophysis (as in Fig. 16 a,b); palpal tibia with proximoventral angular projection (Fig. 16c). Penis (Fig. 18c) essentially straight, parallel-sided over most of length, shaft constricted proximal to slightly inflated glans; alae long, weakly developed. Dorsum yellow-brown to red-brown, eye tubercle and pedal trochanters dark, central figure ranging from absent to evident but weakly contrasting with dorsum (sometimes with fine white outline); usually with transverse bands of small, irregular light spots. Female (Fig. 46): Body 7–8 mm long; free margin of sternum with median notch (Fig. 27a) and genital operculum with transverse furrow and median septum (Fig. 27b), as in *L. euserratipalpe* (Fig. 26a, b) and *L. calcar* (Fig. 25a, b), sternal fultura absent or expressed as posterior thickening of cuticle of pregenital chamber, present in *L. euserratipalpe* (Fig. 26a) and *L. calcar* (25a). Palpal femur and patella brown, lighter proximad and distad; dorsum ranging from yellow-brown to red-brown with central figure dark but variably reduced and fragmented; dark transverse bands sometimes present on scutal tergites 4 and 5; abdominal dorsum often with transverse rows of light and/or dark spots. *Distribution*: Widespread in forests of eastern North America, common in the higher Piedmont and mountains of Maryland, where both sexes move about actively on tree trunks, the leafy understory, and the forest floor.

***Leiobunum politum* (Wood).** *Diagnosis:* Male (Fig. 60): Body ~4 mm long; dorsum and pedal trochanters yellow to red-brown, without central figure; labrum greatly inflated (as in *L. brachiolum*) (Fig. 14c); penis > 2.5 mm long (Fig. 15b, c), subterminal region of shaft with ventral vertical carina and dorsal transverse alae (thus somewhat T-shaped in cross section, as in *L. brachiolum*) but alae extending laterad beyond proximally adjacent lateral wall of shaft. As in *L. brachiolum*, lateral cavities formed by T-shaped apparatus often contain an oval mass of white material (nuptial gift). Female (Fig. 60): Body ~6 mm long; dark central figure potentially extending continuously from anterior margin of carapace to last tergite, but often reduced or enhanced along its path; dorsum otherwise usually a shade of red-brown to purple, abdomen with transverse segmental bands of light flecks on abdomen crossing central figure; pedal trochanters concolorous with base color of dorsum. *Distribution:* Forests throughout eastern and central US and southern Canada, often found moving quickly across forest floor but will also climb leafy vegetation, where it may co-occur with *L. brachiolum*. Aspects of the biology of *L. politum* in Michigan can be found in Edgar (1971).

***Leiobunum uxorium* Crosby and Bishop.** *Diagnosis:* Male (Fig. 42): Body ~4.5 mm long; abdomen truncated to weakly rounded posteriorly; penis short (< 3 mm); as in *L. vittatum*, basal one-half to one-third of shaft wide, remainder thin, cylindrical, glans long and thin (Figs. 6b, 13a). Palpal femur weakly curved, not elongate (Fig. 17b) (distal tip extending to or slightly above the dorsal surface of the eye tubercle), patella somewhat elongate, slightly shorter than tibia; dorsum yellow-orange with yellow and silver flecks (Fig. 42) to uniform brown, central figure poorly developed to absent; eye tubercle and pedal coxae dark. Female (Fig. 41): Body ~6 mm long; as in female *L. vittatum*, anterior external surface with a pair of lateral indentations (li; Fig. 22) corresponding internally to large lateral entapophyses (le), entapophyses meeting or nearly meeting along midline, and anterior transverse sulcus (ts) corresponding internally to transverse median phragma (mp). In contrast to *L. vittatum*, genital operculum essentially flat anteroventrally (Fig. 22), transverse sulcus opening ventrally and median phragma not overlapping lateral entapophyses nor with median trough; coloration bordering dark central figure usually golden brown with light spots and flecks; dark central figure potentially extending from eye tubercle posteriad to last tergite (but often variably reduced), crossed by transverse bands of light flecks; eye tubercle and pedal trochanters dark. *Range:* Recorded from Alabama north through the Atlantic states to Long Island, NY (Bishop 1949), west as far as Ohio and Kentucky; appears to occur throughout Maryland west of the Chesapeake Bay, status on Delmarva unknown. The species was erroneously assigned to *L. speciosum* Banks by McGhee (1970), thus compromising ranges provided for both species by Cokendolpher and Lee (1993). The species is a close relative of *L. vittatum* and can also persist into early winter.

***Leiobunum ventricosum* (Wood).** *Diagnosis:* Male 7–8 mm long, female (Fig. 57) 10–12 mm long; dorsum and pedal trochanters light to golden brown, central figure evident from eye tubercle through scutum, outlined in white (at least anteriorly), may be faded or absent; abdomen somewhat pointed posteriorly, very pointed

in male; labrum ending in simple point (Fig. 14a); penis with subterminal pair of sacs (s; Fig. 12b), with long, dorsoventrally compressed shaft (Fig. 6d). *Distribution*: Eastern North America from southern Canada south to the Gulf Coast, west to the Great Plains. One of the first species to reach maturity in spring in Maryland, persists through summer; most common in moist woodlands. Documented in Allegany (Muma 1945b), Montgomery, Prince Georges, Frederick, and Garrett counties (J.W. Shultz, pers. observ.). It likely occurs throughout the state west of the Chesapeake Bay; no records from Delmarva.

***Leiobunum verrucosum* (Wood.)** *Diagnosis*: Male (Fig. 55): Body ~6 mm long, red-brown dorsally, central figure limited to paired dark lines on first and last scutal tergites; pedal trochanters dark with lighter patches dorsad and ventrad; eye tubercle dark; as in male *L. flavum*, labrum with subterminal pair of lateral tubercles giving arrowhead-like appearance to tip (Fig. 14b) and penis with pair of subterminal sacs (s; Fig. 12a). Female (Fig. 54): Body ~8 mm long, dark brown dorsally with light transverse belt on last scutal tergite, cream ventrally, dark lateral markings; trochanters and eye tubercle dark; femur I comparatively short, subequal to length of body. Dorsal coloration in young adults (April–May) of both sexes with light red-brown base color, prominent dark central figure, and transverse bands of light flecks on abdomen, expect gradations between this and mature coloration (Shultz 2008). Common in late spring on vegetation near woods (especially brambles), tends to move into woods later. *Distribution*: Atlantic Coast of US and southern Canada west to Great Plains; probably occurs throughout Maryland. Aspects of the biology of *L. verrucosum* can be found in Guffey (1998: *L. nigripes*). *Common synonyms*: *L. nigripes* Weed, *L. formosum* (Wood) and *Forbesium formosum* (Wood) correspond to juvenile *L. verrucosum*. See comments on *L. formosum*.

***Leiobunum vittatum* (Say).** *Diagnosis*: Male (Fig. 40): Body ~6 mm; palpal femur long, curved (Figs. 17a), distal tip extending well above dorsal surface of eye tubercle when fully levated; patella and tibia subequal in length; proximoventral surface of tibia more or less inflated, proximal half of tibia with long, spine-like tubercles. Penis long (>3 mm) but otherwise similar to *L. uxorium*: distal two-thirds narrow, cylindrical; proximal third wide, somewhat compressed dorsoventrally (Figs. 6b, 13a). Female (Fig. 40): Body ~8 mm long; as in female *L. uxorium*, anterior external surface with a pair of lateral indentations (li) corresponding internally to large lateral entapophyses (le), entapophyses meeting or nearly meeting along midline and anterior transverse sulcus (ts) corresponding internally to transverse median phragma (mp), but (in contrast to *L. uxorium*) genital operculum (Fig. 21) inflated ventromedially, transverse sulcus opening anteriorly and median phragma overlapping lateral entapophyses. Dorsal color highly variable in time and place in both sexes. *Distribution*: Throughout eastern North America from Atlantic Coast to Great Plains, from southern Canada south to Gulf Coast. Regional variation is significant and may reflect multiple unrecognized species; usually associated with trees or other woody vegetation. The most common and visible of the late-season harvestmen in Maryland; dark, senescent individuals may persist into early winter. *Note*: *Leiobunum crassipalpe* Banks was recorded from Maryland by Muma



(1945b) but the species, as currently understood, is restricted to Missouri, northern Arkansas and eastern Oklahoma (Davis 1934). Maryland records are likely due to misidentification of *L. vittatum*. *Leiobunum speciosum* Banks has been reported from scattered locations throughout the eastern US. However, many specimens in the type series correspond to *L. bimaculatum* Banks, which does not occur in Maryland (closest occurrence is Virginia Beach, VA; Davis 1934; JW. Shultz, pers. observ.). However, the name has since tended to be applied to specimens that are similar to *L. vittatum* but which are predominantly light brown with a posteriorly reduced or obsolete central figure. Populations fitting this description occur near the western coast of the Chesapeake Bay and on the Delmarva Peninsula. The “*speciosum*” morph will be identified as *L. vittatum* here. Further taxonomic work is needed to determine if it and *L. vittatum* are different species. Aspects of the biology of *L. vittatum* are available in Edgar (1971), Fowler-Finn et al. (2014), Guffey (1998), Macías-Ordóñez (2000), and Sensenig and Shultz (2006).

***Nelima elegans* (Weed).** *Diagnosis:* Body 5.5–7.5 mm long; legs long with white banding, tarsi with alternating light and dark bands; cuticle of body soft, largely unarmed; coxae tuberculate but without submarginal anterior and posterior rows of prominent denticles on coxae III and IV, anterior rows may be weakly developed on coxae I and II; eye tubercle dark with median depression; eye tubercle bordered posterolaterally by dark triangular marks; abdominal dorsum with complex and variable bilateral pattern of white, brown and black markings (Fig. 39). *Distribution:* Newfoundland west to South Dakota, southward through New England, the Great Lakes Region, Ohio River Valley, increasingly restricted to Appalachian Mountains farther south; records from Florida, Alabama, and Louisiana require confirmation. Known in Maryland only from Garrett County but may occur farther east, especially in mountains and northern counties. Known to overwinter in aggregations in protected places (caves, under bridges, etc.; see also Moseley and Hebda 2001). *Common synonyms:* *Leiobunum annulatum* Walker, *L. bicolor* Wood, not Fabricius, *L. elegans* Weed.

***Phalangium opilio* L.** *Diagnosis:* Palpal claws without ventral teeth, without trident of prominent spines on anterolateral margin of carapace, palpal femur not armed with retroventral row of large projections. Male (Fig. 37): Body length ~7 mm; penis with large glans capable of being strongly flexed against dorsal surface of shaft (Fig. 6a); palps unusually long; second cheliceral segment with large, proximodorsal conical projection, usually extending anteriorly in life; central figure highly variable, well developed to obsolete. Female (Fig. 38): Body length ~8 mm; dark central figure usually well developed, outlined in white anteriorly; pedal trochanters and base color of dorsum light reddish-brown. *Distribution:* Native to Europe, now widely distributed in temperate regions worldwide, especially in habitats impacted by humans (suburbs, parks, homesteads, agricultural land); probably occurs throughout Maryland in such habitats. There appear to be no previous published records of this species in Maryland, but its absence would be remarkable.

***Odiellus pictus* (Wood).** *Diagnosis:* Body length 5–6.5 mm; palps somewhat robust, claw without ventral teeth, penis with large glans capable of being

strongly flexed against dorsal surface of shaft (Fig. 6a); palpal femur with retroventral row of 8–10 projections (Fig. 35), each with a terminal seta; anteromedial margin of carapace with 3 prominent spines (trident), middle spine longest; eye tubercle armed with prominent tubercles; abdomen extended, end pointed (male) or bluntly rounded (female); metapeltidium and abdominal tergites with a transverse row of low, white tubercles; central figure variably developed; carapace and areas lateral to central figure mottled brown, tan and white. *Distribution*: Canada from Labrador west to Saskatchewan and United States east of Great Plains. In Maryland, known from forests in Garrett and Frederick counties (J.W. Shultz, pers. observ.), probably occurs throughout western Maryland, may occur in appropriate habitats elsewhere in the state; occurs in leaf litter and on tree trunks. This is the first record of *O. pictus* in Maryland, although Muma (1945a) recorded “*Odiellus* sp.” from Garrett County.

***Sabacon cavicolens* (Packard).** Not yet recorded from Maryland. *Diagnosis*: Body length 2–6 mm; palps large with tibia and tarsus inflated, both segments with dense coat of erect setae; palpal tarsus capable of being flexed tightly against tibia (Fig. 34); palpal tarsus without obvious claw; male with five scutal and three free tergites or four scutal and four free tergites; female with all tergites separate, all tergal elements weakly sclerotized, without denticles (see Shear 1975 for details). *Distribution*: Eastern United States and southern Canada in cool, moist habitats, increasingly restricted to mountains in the south; recorded from Pennsylvania, West Virginia, and Virginia (Cokendolpher and Lee 1993, Hedin and McCormack 2017) and expected in Maryland. *Synonyms*: *Phlegmacera cavicolens* Packard, *Sabacon crassipalpe* auct., not of L. Koch (= Asian species).

***Siro exilis* Hoffman.** *Diagnosis*: Small (<3 mm long), somewhat mite-like; dorsum covered by one large sclerite (scutum completum) (Figs. 5a, 28), openings to repugnatorial glands mounted on prominent turrets (ozophores [oz]; Figs. 5a, 28); eyes absent; leg II not significantly longer and thinner than adjacent legs (Figs. 28, 29); pregenital chamber open, not covered entirely by genital operculum (Fig. 29). *Distribution*: Mountains of Virginia, West Virginia, and Maryland in litter and *Sphagnum* in moist forests, often near streams (Shear 1980); known in Maryland only from Swallow Falls State Park in Garrett County (Shear 1980; J.W. Shultz, pers. observ.).

***Vonones sayi* (Simon).** *Diagnosis*: Body ~5 mm long; somewhat pear-shaped in dorsal view, narrow anteriorly, wide posteriorly (Fig. 30); somewhat flattened dorsoventrally; palps appressed to anterior surface of chelicerae in life, palpal tibia flattened, concave ventrally, poorly armed; eye tubercle low, broad. Dorsal color red-brown; scutum magnum (Fig. 5b) variably marked with white-to-yellow lines, usually a V- or Y-shaped mark anteriorly, a transverse line posteriorly, the two sometimes connected by median line, 1 or 2 additional transverse lines (continuous or broken into spots) may occur between the anterior and posterior markings; all lines may be absent. *Distribution*: Atlantic Coast west to Great Plains, south to Gulf Coast and northeastern Mexico, north to southern Illinois, Indiana, Ohio; northern limit on Atlantic Seaboard unknown; also Cuba (Kury 2003). Seems to

prefer well-drained, sandy soils; found during the day under logs, stones, and loose bark. Recorded by the author from Montgomery County near Potomac River and Worcester County near Pokomoke River (J.W. Shultz, pers. observ.); may occur in suitable habitats statewide. This is the first published record of the species in Maryland. Aspects of the biology of *V. sayi* can be found in Cokendolpher and Jones (1991). *Common synonym: Libitoides sayi* (Simon)

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